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In Situ Filtration Rates of Blue Mussels (*Mytilus edulis*) Measured by an Open-Top Chamber Method

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Abstract

Blue mussels, *Mytilus edulis*, form dense beds of both commercial and ecological importance, and many attempts have been made to determine their filtration rate. The total time in which mussels actually utilise their filtration capacity in nature varies greatly, making *in situ* methods for filtration rate measurements relevant. Further, it is being debated to what extend filtration rates measured in the laboratory using cultivated algal cells may apply for mussels in nature. In the present study, we have used an open-top chamber setup in order to allow repeated *in situ* filtration rate measurements of *M. edulis* using ambient natural phytoplankton and free-living bacteria. We found that the *in situ* measured filtration rates are comparable to filtration rates obtained in laboratory studies using different methods and controlled diets of cultivated algal cells. Further, we found that the retention efficiency of free-living bacteria was between 22.2% and 29.9%, in good agreement with values from laboratory studies. Our findings support the assumption that mussels in nature tend to use their filtration capacity when the phytoplankton concentration is above a certain lower trigger level.

Keywords

Bivalvia, Filter-Feeding, Zoobenthos, Valve-Opening Degree, Cultivated Algal Cells, Free-Living Bacteria, Particle Retention Efficiency

1. Introduction

The filter-feeding blue mussel, *Mytilus edulis* (Linnaeus 1758) (Mollusca, Mytilidae), is widely distributed in the North and Mid-Atlantic regions [1] where it frequently forms dense mussel beds of both commercial and ecological impor-

tance [2] [3]. Many attempts have over the years been made to determine the filtration rate of mussels using various methods [2] [3] [4], but it is currently being debated to what extend filtration rates measured in the laboratory using cultivated algae may apply for mussels in nature and whether the filtration rate is physiologically controlled [3] [5].

Laboratory observations of valve gap responses of mussels to absence or presence of added cultivated algal cells to the ambient water have revealed that they close their valves below a lower chlorophyll *a* (Chl *a*) trigger concentration of about 0.9 [6] to 0.5 μg Chl *a* l^{-1} [7]. Likewise, it has been shown that high algal concentrations > 8 μg Chl *a* l^{-1} also induce valve closure, reduce filtration rate [8] and subsequently reduce growth [9]. Under optimal conditions, with algal concentrations between the lower and upper trigger concentrations, mussels tend to filter the ambient water at a maximum rate. Because mussels are often living in dense beds, the ambient Chl *a* may frequently be strongly reduced [10] [11] [12] [13] [14] and likewise, during winter periods with no primary production [15] [16] [17]. The total time in which mussels actually utilise their filtration capacity in nature may therefore vary greatly, making *in situ* methods for filtration rate measurements relevant.

In the present study, we have slightly modified the design of the open-top chamber setup presented by Hansen *et al.* [18] in order to allow repeated filtration rate measurements using the clearance method and ambient natural phytoplankton and free-living bacteria. This approach has also become relevant because Cranford *et al.* [5] have claimed that experiments using added cultivated algal cells stimulate mussels to filter at anomalously high rates. Therefore, the aim of the present work was both to present a modified *in situ* method and to compare *in situ* measured filtration rates of mussels using natural phytoplankton with filtration rates measured in the laboratory using cultivated algal cells. Finally, we attempted to measure the *in situ* retention efficiency of free-living bacteria.

2. Materials and Methods

2.1. Collection of Mussels

Blue mussels (*Mytilus edulis*) were collected in the inlet to Kerteminde Fjord, Denmark, (55˚26'59"N, 10˚39'41"E) in May and June 2018 and cleaned of epifauna. Mussels (L = 35.7 ± 3.4 mm) were placed in groups (n = 10 to 13) on PVC plates in an aquarium with running seawater and allowed to attach themselves with byssus threads for 24 h. Afterwards they were transferred to the open-top chamber.

2.2. Environmental Parameters

Prior to every clearance experiments hydrographic parameters (temperature, salinity and chlorophyll *a* concentration) were measured using a YSI 650 (Yellowstone Scientific Instruments, Big Sky, MT, USA, 6% to 12% uncertainty of Chl *a*

measurements in the used range) at 1 m depth next to the experimental setup. On the experimental days in May and June 2018 (3 days), temperature (T = 17.9 ± 0.9˚C) salinity (S = 17.4 ± 2.0) and chlorophyll *a* concentration (Chl *a* = 3.9 ± 2.5 μg·l^{-1}) varied slightly (n = 18, mean ± SD).

2.3. Open-Top Chamber Setup

The experimental open-top chamber setup used for *in situ* clearance measurements of mussels is depicted in Figure 1. A group of mussels attached to a PVC-plate is placed on the bottom and a transparent acrylic glass tube (d = 29 cm) is subsequently mounted, confining a certain known volume of natural seawater. The water volume in the chamber can be varied by vertical adjustment of the ladder holding the system, which can be submerged down to 90 cm (V_{max} = 60 l; here we used 24.1 ± 5.0 l). Mussels were allowed to acclimate for some hours before the transparent plastic cylinder was mounted (Figure 1) and sometimes kept submerged between the experimental sessions (here several days). Air stones placed at the periphery of the tube ensured efficient water mixing.

Water samples (1 l, 20 μm filtered and preserved in 5 ml Lugol's solution (6% iodine-potassium, 4% iodine solution) and 5 ml preserved in 1.5 ml 1% glutaraldehyde) were taken at discrete time intervals about 10 cm above the bivalves to follow the decrease in algal and bacterial concentrations (C, cells ml^{-1}) as a function of time over a period of 60 min by means of cell enumeration (described below). When the concentration had decreased about 50%, the tube was lifted to allow new seawater to flow in to replace the particle diminished water. Using this procedure, the mussels were minimally distributed. Using the new open-top chamber method almost all disturbing side effects (e.g. changing current velocity, re-suspended algal cells from the sediment and epifaunal co-filtration) that may usually affect *in situ* clearance rate measurements, can be excluded.

2.4. Clearance Rate and Particle Retention Efficiency

The individual clearance rate (Cl_{ind}, l·ind.$^{-1}$·h^{-1}) of a mussel was calculated as (Riisgård *et al.* [8]):

$$Cl_{ind} = V \times b/n \quad (1)$$

Where V = volume of seawater in the open-top chamber (14.5 to 35.7 l), b = slope of regression line in a semi-ln plot for the reduction in algal or bacterial concentration and n = number of mussels. Here, the clearance rate is defined as the volume of water cleared of particles of a certain size per unit of time, and if the particles are retained with 100% efficiency this implies that clearance rate = filtration rate.

Water samples were taken at known time intervals and preserved (see above) for subsequent counting of algal cells in sedimentation chambers (25 ml) using an inverted microscope (Leitz, 400-times magnification). *Rhodomonas salina* (Wislouch, Hill & Wetherbee 1989) and natural phytoplankton concentrations were estimated after 24 h on basis of countings of all phytoplankton cells of one

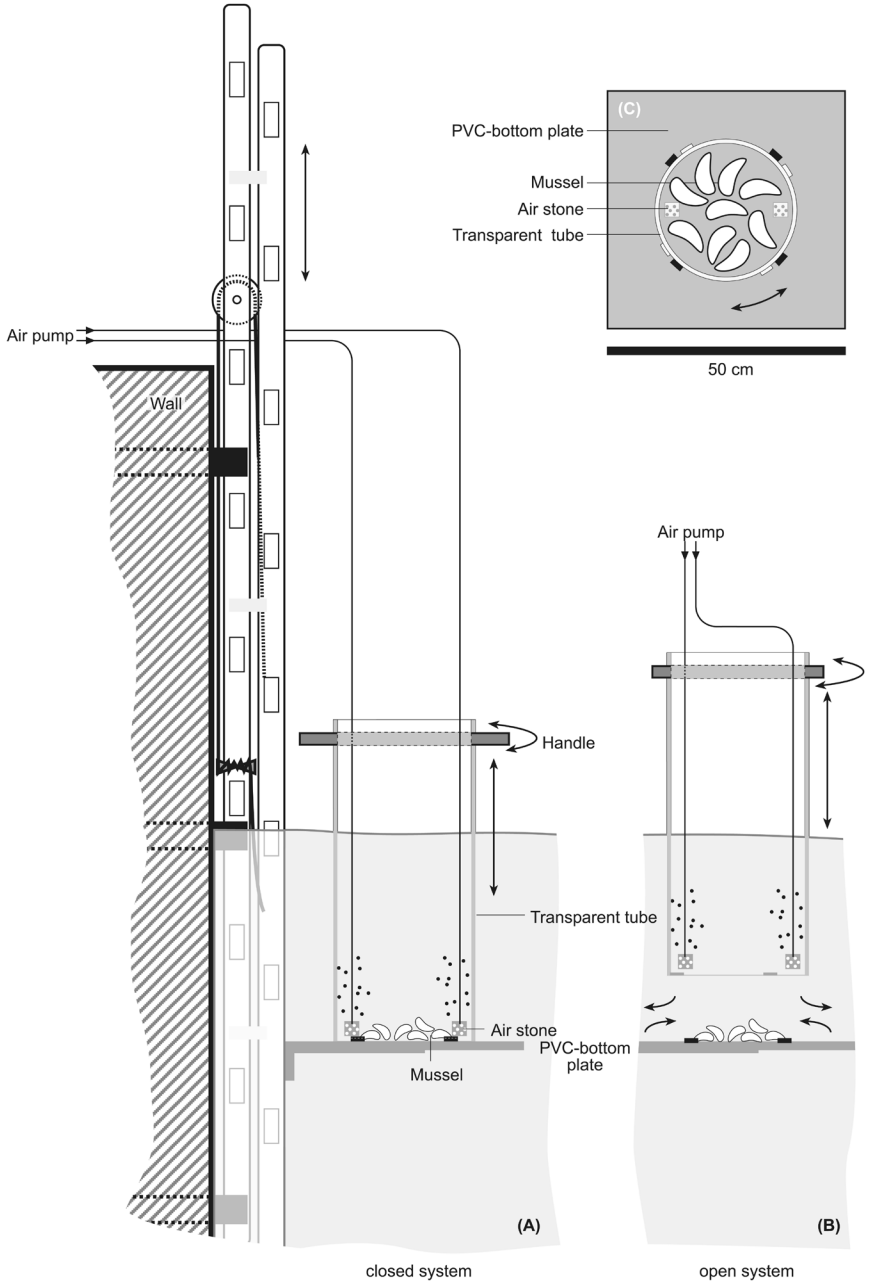

Figure 1. Experimental setup showing closed (A) and open (B) state with the transparent tube-chamber elevated 20 cm above the bottom plate. (C) Top view into the tube-chamber with mussels. Arrows indicate the screwing direction, hoist ropes and water exchange after opening the system.

genus on the bottom plate or *R. salina* cells related to the number of fields of view.

For quantification of the bacteria concentrations in water samples, DAPI staining and epifluorescence microscopy were applied according to Porter & Feig [19]. Thus, 5 ml samples (fixed with glutaraldehyde) were stored in a refrigerator until analysis. Samples were filtered through a 0.2 μm black polycarbonate sheet filter (Whatman Nuclepore Track Etch Membrane) and subse-

quently stained for at least 4 min with 100 µl 4'-6'-diamidino-2-phenylidole (DAPI). When used in combination with epifluorescence microscopy (Leica, type 020-505.030) and UV excitation (Leica Hg-lamp Osram HBO 50 W L2; filter cube A: excitation filter: BP 340 - 380 nm, emission filter: LP 425 nm) individual cells were identified (1000-times magnification), and > 250 bacteria were counted each time according to Muthukrishnan *et al.* [20].

The clearance rate of mussels feeding on *Ceratium* spp. (mainly *C. tripos* and *C. longipes* and to a minor extend *C. fusus*, *C. lineatum* and *C. furca*) and free-living bacteria were measured simultaneously. After 60 min the tube was lifted and surrounding seawater replaced the mussel filtered water. This procedure was repeated up to 5 times (cf. **Figure 2**). After the last clearance rate was measured, the cultured flagellate *Rhodomonas salina* (diameter about 6 µm) was added to the experimental chamber to be grazed by the mussels (up to 3 repetitions). Mussels were observed for shell-opening degree and only open specimens were included in the calculations.

A control with *Rhodomonas salina* showed no reduction of concentration during a period of 60 min (microscopic cell enumeration; cf. **Figure 2(A)** and fluorescence measurements (Aquafluor, Turner Designs, San Jose, CA, USA); data not shown), which demonstrated that the entire reduction in concentration could be attributed to the filter-feeding mussels. The height of the water in the chamber (which changed with the tide) was measured before each experiment in order to calculate the actual water volume. After the experiments, the shell length of mussels (L, mm) was measured using a calliper rule.

The retention efficiency (Re, %) of bacteria was expressed as the ratio of mean clearance rate on bacteria to mean clearance rate of *Ceratium* spp. [21].

2.5. Algal Cultivation

Rhodomonas salina was grown phototrophically (24 h of illumination) in repeated batch cultures at 20˚C in 5 l flasks containing 3 l of seawater (S = 20) enriched with f/2-medium (cf. Guillard & Ryther [22]). Cultures were continuously illuminated by fluorescent light tubes. Aeration and mixing were carried out by injection of compressed air and stirring. Every day, one third of the algal suspension was withdrawn and replaced by fresh medium.

3. Results

Figure 2 shows some typical *in situ* clearance experiments with *Mytilus edulis* feeding on natural phytoplankton (*i.e. Ceratium* spp.), cultured algal cells (*Rhodomonas salina*) and free-living bacteria. The algal concentration was measured as a function of time in 8 series with 5 repeated chamber openings and closings in order to replace the mussel filtered water with new ambient water, followed by 3 repeated algal additions to the chamber now kept closed. The data have been shown in a semi-ln plot of cell concentration *versus* time. The linear regression lines and their slopes b for the different series are shown along with a

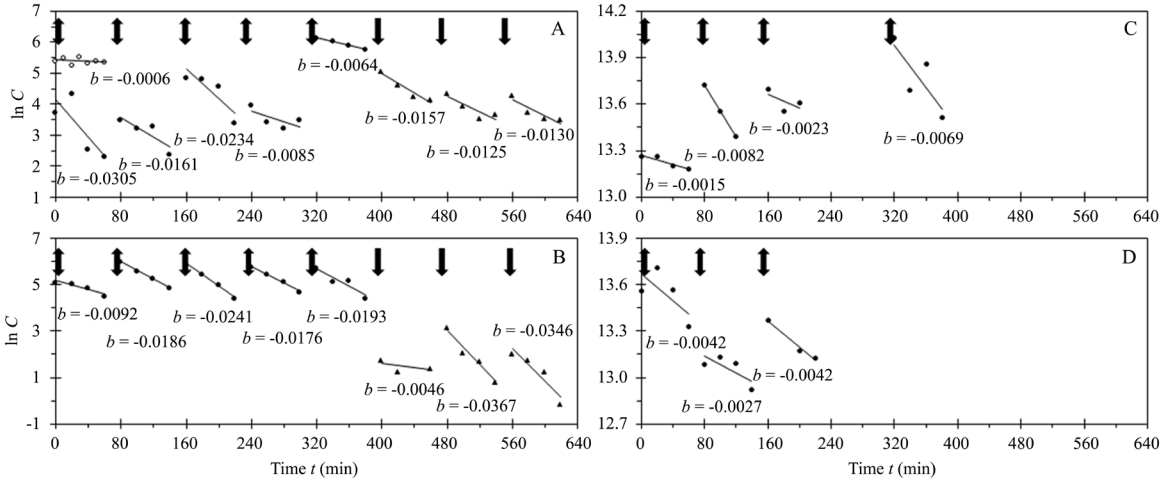

Figure 2. *Mytilus edulis*. Examples of *in situ* clearance experiments with mussels using natural phytoplankton (*i.e. Ceratium* spp.), free-living bacteria and lab-cultured *Rhodomonas salina*. Semi-ln plot of phytoplankton (A, B) and bacteria concentrations (C, D) *versus* time. The slope *b* of the linear regression line for each experiment, started 5 min after either closing the experimental chamber or addition of algal cells, is shown. Filled circles = experiments using natural seawater with phytoplankton and free-living bacteria, filled triangles = experiments with addition of *R. salina*, open circles = control. Two-directional arrows indicate lifting and closing of the tube-chamber. Downward-directed arrows indicate addition of algal culture. Sub-figures A and B display series of clearance experiments with *Ceratium* spp. and *R. salina* on 20 and 25 June 2018 (Table 1). Sub-figures C and D show clearance of bacteria measured simultaneously on these experimental days (Table 2).

control experiment without mussels. The mean (± SD) individual clearance rate of *M. edulis* (L = 35.7 ± 3.4 mm; Figure 2(A) and Figure 2(B)) feeding on *Ceratium* spp. varied between 1.74 ± 0.96 and 2.93 ± 0.93 $l \cdot h^{-1} \cdot ind.^{-1}$ per experimental day (Table 1). Similarly, the mean individual clearance rate of mussels grazing on *R. salina* ranged between 1.94 ± 0.12 and 2.99 ± 2.06 $l \cdot h^{-1} \cdot ind.^{-1}$ per experimental day (Table 1). On the last 2 days, clearance rates of free-living bacteria and *Ceratium* spp. were measured simultaneously and found to be 0.52 ± 0.36 and 0.57 ± 0.17 $l \cdot h^{-1} \cdot ind.^{-1}$ for bacteria (Figure 2(C) and Figure 2(D), Table 2) and 1.74 ± 0.96 and 2.57 ± 0.76 $l \cdot h^{-1} \cdot ind.^{-1}$ for *Ceratium* (Figure 2(A) and Figure 2(B)). Consequently, the retention efficiency was calculated to be 29.9 and 22.2%, respectively (Table 2) (assuming 100% retention efficiency for *Ceratium* spp.).

4. Discussion

From Table 1 it appears that the *in situ* measured clearance rates (= filtration rates) of *Mytilus edulis* are comparable to the filtration rates estimated from the shell length by means of the "model reference equation" presented by Riisgård *et al.* [23] based on available data on *M. edulis* obtained by the same research group using different methods and controlled diets of cultivated algal cells. However, it has been claimed by Cranford *et al.* [5] that experiments using added cultivated algal cells stimulate the mussels to filter at anomalously high clearance rates and that "a major methodological pitfall stems from the application

Table 1. *Mytilus edulis*. *In situ* clearance experiments with various mussel groups and *Ceratium* spp.: Series = running experiment number per day, T = temperature, S = salinity, Chl *a* = chlorophyll *a* concentration, h = height of water column in experimental chamber, n = number of open mussels, L = mean shell length (± SD), V = volume of water in experimental chamber, b = slope of linear regression line (**Figure 2**), R^2 = correlation coefficient, Cl_{ind} = individual clearance rate, Cl_{ref} = individual clearance estimated from the shell length by means of the equation $F_L = 0.00135L^{2.088}$ (Riisgård *et al.* [23]) and used here as a reference for maximum clearance rates measured in the laboratory using cultivated algal cells. * indicates clearance experiments with lab-cultured *Rhodomonas salina*.

Date	Series	T (˚C)	S	Chl *a* ($\mu g \cdot l^{-1}$)	h (cm)	n	L (mm)	V (l)	b (min^{-1})	R^2	Cl_{ind} ($l \cdot h^{-1} \cdot ind.^{-1}$)	Cl_{ref} ($l \cdot h^{-1} \cdot ind.^{-1}$)
21 May	1	18.0	14.2	8.8	34.5	13	35.9 ± 4.8	22.8	0.0216	0.62	2.27	
21 May	2	18.7	12.7	8.1	54.0	13	35.9 ± 4.8	35.7	0.0218	0.98	3.59	
										Mean ± SD	2.93 ± 0.93	2.38
20 June	1	17.8	18.4	3.8	22.0	10	35.3 ± 2.6	14.5	0.0305	0.66	2.66	
20 June	2	17.7	15.9	2.7	29.5	12	35.3 ± 2.6	19.5	0.0161	0.74	1.57	
20 June	3	18.0	15.4	3.8	36.5	12	35.3 ± 2.6	24.1	0.0234	0.76	2.82	
20 June	4	18.5	16.1	4.4	30.5	12	35.3 ± 2.6	20.1	0.0085	0.45	0.86	
20 June	5	18.6	17.5	4.3	37.5	12	35.3 ± 2.6	24.8	0.0064	0.99	0.79	
										Mean ± SD	1.74 ± 0.96	2.30
20 June	6*	19.0	16.6	4.4	38.5	12	35.3 ± 2.6	25.4	0.0157	0.95	2.00	
20 June	7*	19.3	17.3	5.6	43.5	12	35.3 ± 2.6	28.7	0.0125	0.78	1.80	
20 June	8*	19.1	17.6	8.5	47.0	12	35.3 ± 2.6	31.0	0.0130	0.83	2.02	
										Mean ± SD	1.94 ± 0.12	2.30
25 June	1	17.2	16.3	3.1	42.0	10	35.8 ± 2.5	27.7	0.0092	0.86	1.53	
25 June	2	16.1	19.0	2.2	35.0	10	35.8 ± 2.5	23.1	0.0186	0.99	2.58	
25 June	3	16.8	19.2	2.2	38.5	10	35.8 ± 2.5	25.4	0.0241	0.99	3.68	
25 June	4	17.0	19.1	2.0	37.5	10	35.8 ± 2.5	24.8	0.0176	0.99	2.62	
25 June	5	17.2	19.4	1.2	32.0	10	35.8 ± 2.5	21.1	0.0193	0.87	2.45	
										Mean ± SD	2.57 ± 0.76	2.37
25 June	6*	17.3	19.2	1.2	41.0	10	35.8 ± 2.5	27.1	0.0046	0.3	0.75	
25 June	7*	18.0	19.3	1.2	33.0	10	35.8 ± 2.5	21.8	0.0367	0.97	4.80	
25 June	8*	18.3	19.2	2.3	25.0	10	35.8 ± 2.5	16.5	0.0346	0.9	3.43	
Mean ± SD		17.9 ± 0.9	17.4 ± 2.0	3.9 ± 2.5				24.1 ± 5.0			2.99 ± 2.06	2.37

of artificial dietary conditions that stimulate a predetermined (e.g., maximal) feeding response". The presented new data (**Table 1**) clearly disprove this assumption. In the present study, the mussels were exposed to natural phytoplankton occurring in sufficiently high quantities to stimulate the mussels to filter at rates comparable to rates measured on completely open mussels fed cultivated algal cells in the laboratory. The findings support the assumption that mussels in nature tend to use their filtration capacity when undisturbed and the phytoplankton concentration is above the lower trigger level [6] [7] [24]. However, that is frequently not the case, especially in dense mussels beds [6] [10] [11]

Table 2. *Mytilus edulis*. *In situ* clearance experiments with various mussel groups and free-living bacteria: Series = running experimental number per day, h = height of water column in experimental chamber, n = number of open mussels, L = mean shell length (± SD), V = volume of water in experimental chamber, b = slope of linear regression line (**Figure 2**), R^2 = correlation coefficient, Cl_{ind} = individual clearance rate, Re = retention efficiency of bacteria expressed as ratio between mean individual clearance rate of free-living bacteria and algal cells (*Ceratium* spp.).

Date	Series	h (cm)	n	L (mm)	V (l)	b (min^{-1})	R^2	Cl_{ind} (l·h^{-1}·ind.$^{-1}$)	Re (%)
20 June	1	22.0	10	35.3 ± 2.6	14.5	0.0015	0.89	0.13	
20 June	2	29.5	12	35.3 ± 2.6	19.5	0.0082	0.99	0.80	
20 June	3	36.5	12	35.3 ± 2.6	24.1	0.0023	0.40	0.28	
20 June	5	37.5	12	35.3 ± 2.6	24.8	0.0069	0.64	0.85	
							Mean ± SD	0.52 ± 0.36	29.9
25 June	1	42.0	10	35.8 ± 2.5	27.7	0.0042	0.40	0.70	
25 June	2	35.0	10	35.8 ± 2.5	23.1	0.0027	0.55	0.37	
25 June	3	38.5	10	35.8 ± 2.5	25.4	0.0042	0.98	0.64	
							Mean ± SD	0.57 ± 0.17	22.2

and during winter periods with no primary production [17]. During such starvation periods, *M. edulis* reduces its valve gap, and thus the filtration rate in order to save energy by reducing its metabolism [17] [25].

Møhlenberg & Riisgård [26] showed, based on particle size distribution in the inhalant and exhalant water currents, that *M. edulis* and 10 other bivalve species retained particles bigger than 4 µm with 100% efficiency, while particles down to 1 µm were retained with decreasing efficiency (min. about 48%). Likewise, young post-metamorphic *M. edulis* (1 to 4 mm shell length) was found to retain particles down to 4 µm with 100% efficiency, while decreasing to 20% for 1 µm particles [27]. Kreeger & Newell [28] showed in ^{14}C-prey-labeled ingestion and assimilation experiments that *M. edulis* ingested a significantly lower proportion (19%) of bacteria (< 1 µm diameter) than the larger (3 to 5 µm diameter) heterotrophic flagellates (58%). The bacteria (about 0.5 µm diameter) retention efficiency reported by Lucas *et al.* [29] was about 28%. In the present study, the retention efficiency of free-living bacteria was found to be between 22.2 and 29.9% (**Table 2**), which is in good agreement with earlier reported values.

A number of attempts have been made to study the filtration activity of mussels and scallops transferred to laboratory or near natural conditions [30] [31] [32] [33], and mussel behaviour has been recorded *in situ* over time in relation to changing Chl *a* [6] [11] [13]. More recently, Hansen *et al.* [18] used an open-top chamber method designed for *in situ* measurements of community clearance rate on bivalve populations at low water depths (< 0.5 m). In ambient natural seawater, Hansen *et al.* [18] found that an assemblage of bivalves (mussels and oysters) only realised 10% of their theoretical filtration capacity, but when cultivated algal cells were added to the experimental chamber this soon af-

ter increased the filtration activity to 42% of the theoretical (*i.e.* maximum filtration rate measured in the laboratory using cultivated algae by Møhlenberg & Riisgård [34]). Using the same technique developed by Hansen *et al.* [18], Vismann *et al.* [14] found that the filtration rate of *Mytilus edulis* in an intertidal bivalve bed was only about 13% of the theoretical. These findings indicate that the grazing impact of bivalves in shallow water locations may frequently result in depletion of phytoplankton and subsequently closure of the valves and cessation of filtering activity. This interpretation is supported by a recent study by Comeau *et al.* [35] who monitored the valve-opening behaviour of raft-cultivated *M. galloprovincialis* and found that valves were open 97.5% of the time. In agreement with this, our data (**Table 1**) show that *M. edulis* apparently utilises its filtration potential under natural conditions, as long as the Chl *a* level is above the lower trigger concentration.

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Competing Interests

The authors declare no competing interests.

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